INHERITANCE STUDIES WITH KENYA VARIETIES OF *TRITICUM VULGARE* VILL.

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(Plate ii.)

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Introduction.

In recent years new varieties of *Triticum vulgare* Vill. which have a value as a source of resistance to stem rust (*Puccinia graminis Tritici* E. and H.), have been developed in Kenya Colony, East Africa. The resistance of these wheats is unlike that of either Hope or H–44 in that seedlings as well as adult plants are resistant to a large number of physiological races of stem rust. Under similar conditions of temperature, the reaction of seedlings is identical with that of adult plants. In Canada it has been found (Peterson *et al.*, 1940) that these Kenya varieties are practically immune in all stages of growth to several races, but under conditions of high temperature, considerable stem rust may develop on these and other varieties (Newton *et al.*, 1940; Johnson and Newton, 1941).

Australian workers have made extensive use of several varieties of Kenya wheats, and the work reported herein deals with a study mainly carried out at St. Paul, Minnesota, U.S.A., to determine the usefulness of seedling tests on F_3 lines in the greenhouse as a means of predicting the breeding behaviour of these same lines when tested as adult plants in the field. It includes, too, results of a genetical study of the mode of inheritance of resistance to mildew, of the inheritance of awn characters and grass clumps, and a study of the association between these characters.

In an earlier publication the writer (Watson, 1941) reported a high correlation between the seedling and adult plant reaction in material of Kenya parentage, and found that single factors, which were not allelic, governed seedling resistance to race 17 in Kenya 744 and Kenya 745.*

Parental Material.

In this study four varieties were used as parents. Their disease reaction, awn characters and grass clump genotype are given in Table 1.

TABLE 1.
Characters studied in Four Varieties of Wheat.

Variety.	Rust Reaction.	Mildew Reaction.	Awn.	Grass Clump Genotype.†
Kenya 744	Resistant.	Resistant.	Half awned.	aa BB ii gg
Kenya 745	,,	Susceptible.	Tip awned.	
Federation 107	Susceptible.	,,	Beardless.	aa bb II GG
Dundee 985	,,	,,	Tip awned.	aa bb II GG

Crosses were made from parental material that had been carried at the University of Sydney as single plant progenies. Federation 107 and Dundee 985 represent selected strains of these two varieties. The two Kenya varieties were shown by Macindoe (1931) and Waterhouse (1938) to have resistance to race 34 of *Puccinia graminis Tritici.* They were grown at St. Paul for three years, where the reaction varied over that period as shown in Table 2.

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* Varieties carry the University of Sydney Accession Number.

† According to McMillan.

TABLE 2.

Range of Reaction to Stem Rust of Two Varieties of Kenya Wheat tested for Three Years at St. Paul, Minnesota.

Variety.	1938.*	1939.	1940.
Kenya 744	Trace.	Trace.	15–25%
Kenya 745	30%	Trace–30%	25–35%

* The 1938 results are unpublished data furnished by the United States Department of Agriculture, Division of Cereal Crops and Diseases, and the Minnesota Agricultural Experiment Station.

Despite this fluctuation in reaction, the pustules were always of the resistant type. Both varieties at temperatures of 70°–75° F. have been resistant or semi-resistant, as seedlings, to all races of stem rust with which they have been tested.

METHODS.

Crosses were made between the rust resistant and susceptible parents and between the two Kenya varieties in the years 1935, 1936, 1937 and 1938. F_1 plants were grown at Sydney in 1936, 1937 and 1938, and F_2 populations were grown at Richmond, N.S.W., in 1937. F_2 plants, selected at random, were grown as F_3 lines at St. Paul in 1939 and 1940. F_2 plants from the crosses made in 1937, and F_1 plants from those made in 1938, were also grown at St. Paul in 1939. F_3 and F_4 progenies were continued in 1940 from F_2 plants and F_3 progenies respectively, obtained at the 1939 harvest.

Parent varieties were sown along with the hybrid rows. Owing to inadequate seed supply in 1939, they were sown at intervals of one hundred rows, but in 1940 parent rows were grown after each thirty hybrid rows. Parental kernels, and hybrid kernels from all generations, were space-planted three inches apart in rows six feet long.

Stem Rust.

Greenhouse Studies.—F_3 lines and parents of all crosses were tested as seedlings with single races of stem rust in the greenhouse. Inoculations were made by the usual methods. F_2 seedlings from a cross Federation 107 × Kenya 745, which had been tested with race 34 at Sydney, were planted out there. The seed was harvested and random F_3 progenies were tested as seedlings with a number of races singly, and also as adult plants in the field with a mixture of races. F_2 plants of the crosses Federation 107 × Kenya 744, Dundee 985 × Kenya 744, and Kenya 745 × Kenya 744 were grown in the greenhouse, ten kernels being sown in each six-inch pot. These F_2 plants were also inoculated with single races.

Field Studies.—Stem rust epidemics were produced in 1939 and 1940. Thirty-two physiological races were used in 1939, and thirty in 1940. Each race was increased singly in the greenhouse on Little Club, and in June of each year a mixed suspension of uredospores was hypodermically inoculated into susceptible border rows. In 1939 the border rows were of Hard Federation and Marquis, while in 1940 Soft and Hard Federation were sown for this purpose. Identifications of the prevalent races were made each year (Watson, 1942).

F_2 plants were not classified for rust reaction, but plants in F_3 lines were classed into five groups as indicated below, according to the amount of rust present:

1. *Resistant Type* (*R*).—This included types quite free from rust as well as those with some small pustules just above the nodes; an occasional pustule occurred on the neck, but it was never large.

2. *Moderately Resistant Type* (*MR*).—Less resistant than type 1. Small and numerous pustules occurred above the nodes and on parts of the stem. The pustules were never large. Usually 15 to 25 per cent. of the area of the stem was infected.

3. *Semi-resistant Type* (*SR*).—Apparently an intermediate type of reaction. Pustules above the nodes were often quite large, but those on other parts of the stem were much less extensive than in classes 4 and 5. Small pustules occurring on the neck were narrow, and up to 1 mm. in length. Usually 25 to 40 per cent. of the stem was infected.

4. *Moderately Susceptible Type* (*MS*).—All parts of the plant were attacked and the pustules were numerous. They were smaller than those of class 5. From 40 to 60 per cent. of the stem was covered.

5. *Susceptible Type* (*S*).—Large confluent pustules occurred on all parts of the stem and leaves. All parts of the plant were readily attacked, and long broad pustules appeared on the neck. Plants having over 60 per cent. of the stem area covered were placed in this group.

The Kenya varieties and homozygous resistant lines were more resistant in 1939 than in 1940. In the former year, classes R, MR, SR and S were used, and F_3 lines were grouped on this basis:

R	Breeding true for resistance.
R–MR	Segregating with resistant and moderately resistant plants.
R–SR	Segregating with resistant and semi-resistant plants.
R–S	Segregating with resistant and susceptible plants.
SR–S	Segregating with semi-resistant and susceptible plants.
S	Breeding true for susceptibility.

In 1940, since more rust developed, it was necessary to use the following additional rust classes:

MR	Breeding true for moderate resistance.
SR	Breeding true for semi-resistance.
MR–S	Segregating with moderately resistant and susceptible plants.
MR–MS	Segregating with moderately resistant and moderately susceptible plants.
SR–MS	Segregating with semi-resistant and moderately susceptible plants.
MS–S	Segregating with moderately susceptible and susceptible plants.

Powdery Mildew.

After notes had been taken for rust reactions on seedling F_2 plants and F_3 lines, they were removed to a separate greenhouse where they were inoculated with a single race of *Erysiphe graminis Tritici.* This race is unlike the two races previously described in the United States (Mains, 1933), in that it attacks Vernal Emmer. Classification for mildew reaction was very simple, and the F_3 lines were grouped as immune like the Kenya 744 parent, as segregating, or as susceptible like the susceptible parent.

Awns and Grass Clumps.

F_2 populations sown in the greenhouse were classified as seedlings for their disease reaction and as adult plants for awn development and height. F_3 progenies were classified in the field. No progenies of grass clumps were grown to F_3 since many grass clumps did not even produce heads, and from those that did, only 2–3 grains were obtained.

EXPERIMENTAL RESULTS.

1. *Field Studies with Stem Rust in 1939–1940.*

In 1939, F_1, F_2, F_3 and parental material were grown in the field.

F_1 Results.—F_1 generations of all crosses, except Federation 107 × Kenya 745, were tested in the field at St. Paul. In the crosses with Federation 107 × Kenya 744, and between Dundee 985 and both the Kenya varieties, the reaction of F_1 plants was intermediate between that of the two parents. In the cross involving the two Kenya varieties, the F_1 plants were no more susceptible than the Kenya 745 parent. It was impossible to determine whether the resistance of either parent was dominant.

F_2 Results.—Single F_2 plants were harvested at Richmond in 1937 and at Sydney in 1938, but no classification for rust reaction was made. The F_2 populations grown at St. Paul were treated similarly and the genotype of F_2 plants determined by their breeding behaviour in F_3.

F_3 Results.—All notes on mature plants were taken in the field. Parent rows were classified along with the hybrids and their reaction is given in Table 3 and Plate ii, fig. 1.

In 1939, the classification was on the basis of plants, while that in 1940 was on a row basis. Of the 85 resistant plants of Kenya 745 some showed complete absence of rust, others had up to 15 per cent. Six plants of this variety which had been spaced 8 inches apart to obtain maximum yield of grain, showed up to 30 per cent. of rust on the northern shady side of the stem and almost complete absence of pustules on the southern sunny side. Since these plants were grown under abnormal conditions, their reactions were not included as typical of the parents. Stems of such plants, as well as those of certain

TABLE 3.

Range of Reaction of Four Parental Varieties of Wheat grown in Two Years at St. Paul, Minnesota.

Variety.	Number of Plants or Rows classified in Each Group.				
	1939 (Plants).		1940 (Rows).		
	R.	S.	MR.	SR.	S.
Kenya 744 ..	115		13		
Kenya 745 ..	85			18	
Federation 107		92			23
Dundee 985 ..		135			9

of the hybrids, are figured in Plate ii, fig. 2. Unequal development of rust on two sides of a stem has been observed at St. Paul for many years, and it has also been reported by Waterhouse (1938). The cause has not yet been determined, but it is interesting to note that whereas Waterhouse found the greatest development to occur on the northern or sunny side of the stems, at St. Paul rust was always more abundant on the northern or shady side of the stems.

(i). *Federation 107 × Kenya 744.*—In Table 4 are given the reactions of F_3 lines of this cross.

TABLE 4.

Reaction of F_3 Lines of the Cross Federation 107 × Kenya 744 tested as Adult Plants to a Collection of Physiological Races of Stem Rust in 1939 and 1940.

	Year.	Number of Lines classified in Each Group.									
		R.	R-MR.	MR.	R-S.	MR-S.	MR-MS.	SR-S.	MS-S.	S.	Total.
Federation 107 × Kenya 744.	1939	23	18		80			3		15	139
	1940			63		95	1		2	47	208

The F_3 lines fall into five classes, and in 1939, 23 lines were as resistant as Kenya 744, and 15 as susceptible as Federation 107. By grouping the R and R–MR lines together and regarding those in the classes SR–S as susceptible, the results do not agree very closely to a 1:2:1 ratio for this year. The Kenya 744 parent when sown between 29th April and 2nd May at St. Paul had headed out by 23rd June. It became apparent that some of the lines had escaped rust infection, and it was at first thought that earliness may have partly accounted for the little rust on the Kenya 744 parent. Some F_3 lines, whose 1939 classification was known, were grown as F_4 in 1940, the progeny of a number of plants being bulked to give a composite F_4 row. The figures in Table 5 show that 7 of the 18 families grown to F_4 had been wrongly classified in F_3.

TABLE 5.

The Breeding Behaviour of Tested F_3 Lines grown and tested in F_4.

		F_4 Classification.			
		MR.	MR-S.	S.	Total.
F_3 Classification.	R.	2	1	1	4
	R-SR.		2		2
	R-S.	1	4	1	6
	S.		1	5	6
	Total ..	3	8	7	18

This could be explained on the basis of a difference in the rust races present in the two years, or it could have been due to a difference in environmental conditions. The most likely interpretation, however, is that some plants escaped infection in 1939.

The field test in 1940 was more satisfactory than in the previous year. Rust developed earlier, and little difficulty was experienced in classifying lines that were homozygous susceptible. The Kenya 744 parent was less resistant than in the previous year, and 13 rows were classified as moderately resistant. Twenty-three rows of Federation 107 were susceptible. Among the 208 F_3 families was one with moderately resistant and moderately susceptible plants. This family was considered to be a true representative of the MR–S class, since its seedlings segregated for resistance and susceptibility to race 36. The two families in the MS–S group were from seedlings which were fully susceptible to race 36 and hence they probably belong to the S group.

If the MR–S and MR–MS classes are grouped and the two MS–S lines are placed with the homozygous susceptible, a ratio of 63 moderately resistant : 96 segregating : 49 susceptible lines is obtained. This closely approximates a 1:2:1 ratio, and indicates that a single major factor differentiates resistance, or moderate resistance, from susceptibility in this cross, when the lines are tested as adult plants in the field.

(ii). *Federation 107 × Kenya 745.*—A fairly accurate classification of F_3 lines of this cross was obtained both in 1939 and 1940. The Kenya 745 parent matures later at St. Paul than Kenya 744, and has been found to be less resistant to stem rust over a period of three years. In addition, stems of this variety have less structural resistance than Kenya 744 (unpublished data). Tested F_3 lines of this cross were placed in five groups as shown in Table 6.

TABLE 6.

Reaction of F_3 Lines of the Cross Federation 107 × Kenya 745 tested as Adult Plants to a Collection of Races in 1939 and 1940.

——	Year.	Number of Lines classified in Each Group.								
		R.	R-SR.	SR.	R-S.	SR-MS.	SR-S.	MS-S.	S.	Total.
Federation 107 × Kenya 745	1939	49	12		99		4		35	199
	1940			64		1	148	2	62	277

Tests of seedlings of the 12 R–SR lines showed that 7 of them were homozygous resistant to race 17, and 5 segregated. The 4 lines of the SR–S group were homozygous susceptible as seedlings when inoculated with race 17. Five of the lines in the R–S group were homozygous susceptible. The reaction of F_4 progenies confirmed the inaccuracies found by the seedling test.

Eighteen rows of Kenya 745 were grouped as semi-resistant in 1940, the rust on the stems varying from 25 to 30 per cent. of the total area. The results of tests with F_3 lines are given in Table 6. One line which was segregating in its seedling reaction to race 17 was classed as segregating in the field, but in the SR–MS group, since plants within this line did not show the full susceptibility of Federation 107. Two lines homozygous susceptible as seedlings to races 17 and 56 were placed in the MS–S class, since no plants had semi-resistance equal to that of Kenya 745, and some were less susceptible than Federation 107. The corrected 1939 results, and those for 1940, indicate a single major factor in Kenya 745 for stem rust resistance in the field.

In crosses where Dundee 985 was used as the susceptible parent, results similar to the above were obtained, and gave strong evidence to indicate the presence of a single major factor in each of the Kenya parents. In this case, too, there was a deficiency of homozygous susceptible families in 1939, and was accounted for by the inadequate development of rust in that year. From this field study it is apparent that certain minor factors, as many investigators have found in other studies, can be of importance.

Undoubtedly some of these minor factors segregate independently of the major, and, as a result, pure breeding F_3 lines can arise which have a type of resistance or susceptibility unlike that of either parent.

2. *Greenhouse Studies with Seedling Resistance to Nineteen Races of Stem Rust.*

At temperatures ranging from 70°–75° F. both Kenya varieties have been resistant or semi-resistant as seedlings to all races of stem rust with which they have been tested. At these temperatures it is not always easy to distinguish between the reaction given by these two varieties. If the temperature is raised to 80°–85° F., Kenya 744 is distinctly less resistant than Kenya 745 when inoculated with races 15, 17, 19, 34, 36, 38, 56, 69, 80, 117 and 147. As almost all of the work was done during the cooler months of 1939 and 1940, both varieties were quite resistant. Kenya 745 gave reactions that varied on the same leaf from flecks to type 2 pustules when tested with races 1, 11, 14, 17, 19, 21, 34, 36, 38, 47, 49, 56, 59, 69, 80, 97, 117, 147, and two cultures of race 15. One culture, a virulent biotype of race 15 from Brazil (Loegering and Stakman, 1942), gave type 2+ uredosori on Kenya 745.

Kenya 744 has not been tested so extensively as the 745 parent, but with those races that have been used, the range of reaction was from type 1++ to type 2+. Federation 107 has already been shown to be susceptible to six physiological races of stem rust in Australia (Waterhouse, 1938), and Dundee 985 is considered somewhat similar in its reaction (unpublished data). Both Federation 107 and Dundee 985 were tested with a number of races in the United States. The former has a type 4 reaction with races 1, 11, 14 (two cultures), 15 (three cultures), 17, 21, 34, 36, 38 (one culture), 47, 49, 56, 59, 80, 97, 117 and 147. With races 19, 69 and one culture of race 38, Federation 107 showed a moderately resistant reaction at 70°F. Dundee 985 was not tested to all these races, but gave type 3+ reactions with races 11, 15, 17, 19, 34, 38, 56, when incubated at 70° F.

(i). *Federation 107 × Kenya 744.*—F_2 plants and F_3 lines were inoculated as seedlings with single races in the greenhouse, and with the particular races used, it was found that a single factor differentiated resistance from susceptibility in each case. When 268 plants were inoculated with race 56, 198 of them were resistant and 70 were susceptible. A population of 80 plants gave 60 resistant and 20 susceptible when tested with race 17. Seedling F_3 lines, when tested with races 17, 36 and 56, confirmed the presence of a single major factor for rust resistance in Kenya 744. Moreover, it was found that one and the same factor operated against all three races.

(ii). *Federation 107 × Kenya 745.*—This cross has been studied more extensively than any other. Hybrids derived from it have been more desirable agronomically than those derived from Kenya 744, and in New South Wales, the Kenya 745 parent has been considered to have resistance under a wider range of conditions. At the University of Sydney, 214 F_2 plants of this cross were tested as seedlings with an Australian culture of race 34, designated as the standard Australian biotype of that race (Waterhouse and Watson, 1941). Each plant was classed into one of three groups: resistant, semi-resistant and susceptible. These seedlings were transplanted and harvested singly. The progeny of these, in addition to that of 81 others which escaped infection as F_2, were tested as seedlings at St. Paul with either race 17 or 56, or both. Their behaviour in relation to the F_2 classification is given in Table 7.

TABLE 7.

The Breeding Behaviour of F_2 Plants of the Cross Federation 107 × Kenya 745 to Two Races of Puccinia graminis Tritici.

		F_3 Reactions to Races 17 and 56.			
		Resistant.	Segregating.	Susceptible.	Total.
Reaction of F_2 Plants to an Australian Biotype of Race 34.	Resistant.	55	85	3	143
	Semi-resistant.		23		23
	Susceptible.		1	47	48
Total		55	109	50	214

Among the 143 F_2 plants classified as resistant to race 34, three were pure breeding susceptible when their progeny was tested with races 17 and 56. If different genetic factors governed resistance to the above culture of race 34 and to race 56, and if these were inherited independently, or so linked as to allow recombinations, then such a homozygous class could be expected. When the three progenies were tested with a culture of race 34 from the United States, all were homozygous susceptible. It seems most likely that an error was made in the original classification as F_2 seedlings. One of the susceptible F_2 plants segregated for resistance and susceptibility, but the remaining 47 bred true as expected.

Of the 295 families tested in this cross, 280 were inoculated with both races, and 278 of these gave identical reactions with both races. The discrepancy in one of these families was traced to an error in seedling classification, but that in the other was not accounted for. It is considered that the close agreement in the results gives conclusive evidence that the same gene in Kenya 745 gives resistance to races 17 and 56.

F_3 lines whose reactions to races 17 and 56 were known, were selected and tested with a group of races that were isolated from the 1939 rust nursery, and to some additional races. Only small numbers of lines were used, comparable with those used by Aamodt (1923, 1934) in his study of the genetics of resistance in a Kanred × Marquis cross. From this test it was found that lines homozygous resistant or homozygous susceptible to races 17 and 56 gave this same reaction when tested with races 1, 11, 14 (one culture), 15 (two cultures), 17, 21, 34, 36, 47, 49, 56, 69, 80, 97, 117 and 147.

(iii). *Dundee 985 × Kenya 744.*—F_2 plants and F_3 lines of this cross, when inoculated with race 17, again indicated a single major factor for resistance.

(iv). *Dundee 985 × Kenya 745.*—This result was similar to that obtained in the Federation 107 × Kenya 745 cross, and indicated a single major factor for resistance to race 17.

(v). *Kenya 745 × Kenya 744.*—Two hundred and twenty-seven F_2 plants of this cross were inoculated as seedlings with race 17, and were classified into one of two groups, resistant and susceptible. The resistant class comprised those plants varying in reaction within the limits of the two parents. Of the number tested, 209 were resistant and 18 susceptible, a fairly close fit to a 15:1 ratio. At the time of testing this material, Kenya 744 showed flecks and type 2+ reactions, and Kenya 745 showed only flecks with race 17. When 342 random F_3 lines were tested, they were divided into six classes as presented in Table 8.

TABLE 8.

Observed and Calculated Ratios of Seedlings of F_3 Lines of the Cross Kenya 745 × Kenya 744 when inoculated with Race 17 of Puccinia graminis Tritici.

	Resistant.			Segregating.		Susceptible.
	;	; and 2+	2+	; and 3+	2+ and 3+	3+
	49	74	19	147	31	22
Observed	142			178		22
Calculated 7 : 8 : 1	149·62			171·00		21·38

P value for agreement with a 7 : 8 : 1 ratio lies between 0·30 and 0·50.

The results obtained both in F_2 and F_3 can be explained on the basis that seedling resistance to race 17 is controlled by a single major factor in each of the resistant parents, and that these factors are inherited independently, so that the double recessive class is susceptible as shown in Plate ii, fig. 3. While this simple explanation is tenable in the case of race 17, preliminary work, which will be more fully reported later, indicated that it will not hold when race 45 is used, since 59 random F_3 lines, involving approximately 1,500 plants, did not yield a homozygous susceptible family.

3. *Seedling Resistance to Other Races and Biotypes within Races.*

It has previously been pointed out (Watson, 1941) that Federation 107 is moderately resistant to race 38, and that the gene for moderate resistance to this race is allelic to the gene for resistance in Kenya 745. When 85 F_3 lines of a cross between these two were tested to this culture of race 38 (designated here as race 38A), it was very clear that a single major factor governed resistance to it. In these 85 lines none was obtained more susceptible than Federation 107, and all those that were homozygous susceptible to race 56 were homozygous for moderate resistance to race 38A. From this it was apparent that the same gene in Kenya 745 governed resistance to race 56 and to race 38A.

Seedlings of Federation 107 are susceptible to race 19, but less so than to races 17 and 56. Twenty-nine random F_3 lines of the cross Federation 107 × Kenya 745, previously tested with races 17 and 56, were inoculated with race 19, and the distribution of the lines is given in Table 9.

TABLE 9.

Distribution of 29 Random F_3 Lines of the Cross Federation 107 × Kenya 745 for Their Reaction to Races 17, 19 and 56.

		Reaction to Races 17 and 56.			
		Resistant.	Segregating.	Susceptible.	Total.
Reaction to Race 19.	Resistant.	6	6	1	13
	Segregating.		9	6	15
	Susceptible.			1	1
Total		6	15	8	29

Among the 15 families which segregated for resistance to race 19, five segregated in a ratio approximating 15:1 and ten in a ratio approximating 3:1.

The result can be explained if two independent factors K_1 and K_2 are assumed to be present in Kenya 745, either of which, in the homozygous or heterozygous condition, can give resistance to race 19. One of these, the factor K_1, gives resistance to races 17 and 56 as well as to the other races mentioned previously. According to theory these two would segregate in F_2, so that F_3 progenies would react as shown in Table 10.

TABLE 10.

Genotype of F_2 Plants and Their Expected Breeding Behaviour to Three Races of Stem Rust.

	Breeding Behaviour in F_3 to Races:	
Genotype of F_2 Plant.	17 and 56.	19.
$K_1\ K_1\ K_2\ K_2$	Homozygous resistant.	Homozygous resistant.
$K_1\ K_1\ K_2\ k_2$	,, ,,	,, ,,
$K_1\ k_1\ K_2\ K_2$	Segregating.	,, ,,
$K_1\ k_1\ K_2\ k_2$	,,	Segregating.
$K_1\ K_1\ k_2\ k_2$	Homozygous resistant.	Homozygous resistant.
$K_1\ k_1\ k_2\ k_2$	Segregating.	Segregating.
$k_1\ k_1\ K_2\ K_2$	Homozygous susceptible.	Homozygous resistant.
$k_1\ k_1\ K_2\ k_2$	,, ,,	Segregating.
$k_1\ k_1\ k_2\ k_2$	,, ,,	Homozygous susceptible.

A type of segregation in agreement with this theory was obtained when lines were inoculated with race 14A (a culture of race 14 isolated from barberry in Pennsylvania), with race 59, and with 38B (a culture of race 38 isolated from the rust nursery at University Farm in 1939). Lines whose seedling reaction to this latter race was known, were grown under an epiphytotic of race 34 in the field at Richmond, N.S.W., in 1942, and the combined segregation for field reaction to race 34 and seedling reaction to race 38B, is given in Table 11.

On the basis of the scheme given in Table 10, the expected number of lines falling into each class can be found, and when the observed and expected are compared, the χ^2 value of 6·566 indicates a good agreement.

TABLE 11.
Observed and Calculated Distribution of 110 F_3 Lines of a Cross Federation 107 × Kenya 745 for Their Reaction to Race 34 in the Field, and to Race 38B in the Greenhouse.

	Reaction to Race 34 in the Field.			
Reaction to Race 38B.	Resistant.	Segregating.	Susceptible.	Total.
Resistant	19 (27·50)*	19 (13·75)	6 (6·875)	44 (48·125)
Segregating		40 (41·25)	16 (13·75)	56 (55·00)
Susceptible			10 (6·875)	10 (6·875)
Total	19 (27·5)	59 (55·0)	32 (27·5)	110 (110·00)

The factors K_1 and K_2 are not equal in the degree of resistance they impart to the plant. Homozygous lines of the genotype $K_1K_1k_2k_2$ which have been isolated are much more resistant to race 38B than are those of the genotype $k_1k_1K_2K_2$. Under glasshouse conditions of 75°–85°F. the former are characterized by a fleck and type 1– reaction, the latter by a type 2– or 2+ reaction.

It appears then that Kenya 745 has two factors for resistance to race 38B, but only one for resistance to 38A. F_3 lines can therefore be used to separate out biotypes within races. Federation 107 will also separate these biotypes 38A and 38B, which on the differentials, appear alike.

Two cultures of race 14, both isolated from barberry, were compared in the same way. One, race 14A, was from barberry collected in Pennsylvania, and was kindly supplied by Dr. E. C. Stakman and Mr. W. Q. Loegering, and the second, race 14B, was from barberry grown at University Farm, and was furnished through the courtesy of Dr. R. U. Cotter. Both cultures were race 14 on the standard 12 varieties, and the culture from University Farm was only slightly more virulent on Federation 107 than the culture from Pennsylvania. Federation 107 was susceptible and Kenya 745 was resistant to both 14A and 14B.

When F_3 lines, previously tested with races 17 and 56, were inoculated with these two cultures, the results were strikingly different. Fourteen lines were tested with race 14A and 34 with race 14B, and the results are given in Table 12.

TABLE 12.
Distribution of F_3 Lines of the Cross Federation 107 × Kenya 745 for Reaction to Races 17 and 56, and to Two Cultures of Race 14.

		Reaction to Races 17 and 56.		
		Resistant.	Segregating.	Susceptible.
Reaction to Race 14A.	Resistant.	9		
	Segregating.			4
	Susceptible.			1
Reaction to Race 14B.	Resistant.	5		
	Segregating.		18	
	Susceptible.			11

From Table 12 it is clear that race 14B gave results in complete agreement with those obtained with races 17 and 56. It was concluded that the same factor controlled resistance to all three. Although only a small number of families was tested to race 14A, the reactions were very definite. Nine of the lines selected for their resistance to races 17 and 56 were also resistant to race 14A. However, of the five lines susceptible to races 17 and 56, four segregated and one was homozygous susceptible.

In addition to comparing biotypes of races within the United States, three collections of race 15 were made available to the writer by E. C. Stakman and W. Q. Loegering. They represented biotypes from Brazil, Japan and the United States. Difference in their virulence had been observed previously when these isolates were placed on the

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* Figures in parentheses indicate calculated frequencies.

12 standard differential varieties (Loegering and Stakman, 1942). Differences were also observed when all three were placed on Kenya 745 and Federation 107 as shown in Plate ii, fig. 4. Both varieties gave an identical reaction when inoculated with the culture from Japan and that from the United States. When the Brazilian culture was used, the reaction on Federation 107 was normal, but on Kenya 745 it proved to be the most virulent culture with which this variety had been inoculated. In contrast to the fleck and type 2– reactions, obtained when it was inoculated with the Japanese and American isolates of race 15, the reaction to the Brazilian culture was designated type 2+. Kenya 745 could not be regarded as susceptible to this isolate, but its differential reaction was pronounced.

A number of random F_3 lines of the cross Federation 107 × Kenya 745 was inoculated with these three cultures. The progeny of each F_2 plant was divided so that 25 seeds could be sown in the field. Not all F_2 plants gave enough seed to allow the four tests. The distributions are given in Tables 13, 14, 15 and 16.

TABLE 13.
Distribution of F_3 Lines of the Cross Federation 107 × Kenya 745 for Reaction to Two Cultures of Race 15.

		Reaction to Japanese Culture.		
		Resistant.	Segregating.	Susceptible.
Reaction to United States Culture.	Resistant.	7		
	Segregating.		16	
	Susceptible.			10

TABLE 14.
Distribution of F_3 Lines of the Cross Federation 107 × Kenya 745 for Reaction to Two Cultures of Race 15.

		Reaction to Japanese Culture.		
		Resistant.	Segregating.	Susceptible.
Reaction to Brazilian Culture.	Semi-resistant.	1	2	4
	Segregating.	4	15	7
	Susceptible.		3	2

TABLE 15.
Distribution of F_3 Lines of the Cross Federation 107 × Kenya 745 for Reaction to Two Cultures of Race 15.

		Reaction to United States Culture.		
		Resistant.	Segregating.	Susceptible.
Reaction to Brazilian Culture.	Semi-resistant.	1	2	3
	Segregating.	2	16	4
	Susceptible.	1	5	3

TABLE 16.
Distribution of F_3 Lines of the Cross Federation 107 × Kenya 745 for Their Combined Reaction to Cultures of Race 15 from the United States, Japan and Brazil.

		Reaction to the United States Culture and/or the Japanese Culture.			
		Resistant.	Segregating.	Susceptible.	Total.
Reaction to Brazilian Culture.	Semi-resistant	1	3	4	8
	Segregating.	4	22	6	32
	Susceptible.	1	6	4	11
Total ..	.. .. ..	6	31	14	51

In those cases where inadequate seed was available for testing all three cultures on the one F_3 line, the cultures were compared two at a time. No differences were found with the lines tested with the cultures from the United States and Japan, and it was assumed the same gene in Kenya 745 governed resistance to both. Thirty-eight comparisons were made between the Japanese and the Brazilian cultures and 37 between the cultures from the United States and from Brazil, the data being given in Tables 14 and 15. Since no deviation was observed when random lines were inoculated with cultures from Japan and the United States, the comparisons of each of these with that of the Brazilian culture are brought together into the composite Table 16.

The numbers of lines tested with each of the cultures are small, but their reaction to the Brazilian culture is different from the reaction to the cultures from Japan and the United States. It is possible to explain this by assuming that the gene in Kenya 745 giving resistance to the Japanese and American isolates of race 15, is ineffective against the culture of race 15 from Brazil. This Kenya parent, however, has a minor factor that offers partial resistance against this Brazilian culture.

The results with races 14, 15 and 38 indicate that just as great a genetical difference can be obtained when different isolates of one race are used on F_3 lines as have been obtained when different races are used. In this respect, the results presented are not unlike those obtained previously by other workers. In a cross between H–44–24 and Marquis, it was found (Goulden, Neatby and Welsh, 1928) that the same factors, or ones closely linked to them, governed the reactions to races 14, 17 and 21, and that the factors for resistance to race 36 were distinct from those governing resistance to the other group. Neatby (1931), in analysing the factor relations in the same cross, showed that two sets of factors, each of only one pair, were operative in resistance. One pair affected the reactions to races 35, 36, 49, 52 and 57, and to races 14, 15, 21, 29, 30, 48 and 53. The other pair affected reactions to races 27, 33 and 50, and to races 35, 36, 49, 52 and 57.

In all tests previously made on hybrid material by other workers, races have been used that can be sharply differentiated on the varieties selected by Stakman and Levine (1938). Extensive work on other fungi, however, shows that a single parasitic race can be separated into a number of biotypes on the basis of the characters of the latter when grown in artificial culture. From the work of previous investigators, and from the results reported here, it is clear that isolates within a physiological race of stem rust also differ markedly genetically, although not sufficiently to have them placed as separate races on the basis of their reaction on twelve differential varieties.

4. *Resistance to Powdery Mildew in the Greenhouse.*

Kenya 744 was immune to both races of *Erysiphe graminis Tritici* present in the greenhouses at St. Paul. One of these races is unlike either of the two previously described in the United States (Mains, 1933), in that it attacks Vernal Emmer. Kenya 745, Federation 107 and Dundee 985 were also susceptible. F_2 plants, and F_3 lines of certain of the crosses involving Kenya 744, were inoculated with a single race of mildew, namely, that to which Vernal Emmer is susceptible.

When F_2 plants were inoculated in the greenhouse, there was no difficulty in classifying those susceptible like the susceptible parent. The resistant plants were of two types: those completely immune like the Kenya 744 parent, and those having several mildew pustules on some part of the stem. In the seedling stage, however, when this classification was made, there were only two classes, immune and susceptible. Immunity was assumed to be dominant, since that has been found to be the case with these same crosses, when tested for mildew reaction in F_1 at the University of Sydney.

In Table 17 are presented the results of the inoculations, and it is clear that a single major factor governs resistance in each case.

Correlation studies on the resistance of seedling plants of wheat to *Puccinia graminis Tritici* have been extensive, but adult plant resistance to *Erysiphe graminis Tritici* has not been well demonstrated. In connection with this, an attempt was made to induce an epiphytotic of powdery mildew in the field in 1940, but without success. Border rows of Soft Federation became heavily infected, but owing to lack of density in F_3 spaced rows, mildew did not develop uniformly on the susceptible lines.

TABLE 17.

Genetic Ratios obtained when F_2 Plants and F_3 Lines of Crosses involving Kenya 744 were inoculated with a Single Race of Erysiphe graminis Tritici.

Cross.	F_2 Plants. Res. Susc.	Range of P Value.	F_3 Lines. Res. Seg. Susc.	Range of P Value.
Federation 107 × Kenya 744 ..	539 : 219	0·01–0·02	37 : 68 : 39	0·70–0·80
Dundee 985 × Kenya 744 ..	518 : 144	0·05–0·10		
Kenya 745 × Kenya 744 ..	246 : 65	0·05–0·10	109 : 186 : 80	0·10–0·20

Parent plants and random F_3 lines of each of the crosses given in Table 17, were grown in six-inch pots in the greenhouse. Inoculations were made after the plants had developed their second leaf, and on susceptible plants the infection spread until the plants were mature. Kenya 744 was immune, both as seedlings and as adult plants. The three susceptible varieties were susceptible at all stages of growth, Dundee 985 and Kenya 745 being somewhat less susceptible than Federation 107. Frequent dustings with sulphur were necessary to allow this latter variety to produce heads. Conidia were abundant, but no perithecia developed.

Among the F_3 lines that were homozygous resistant like the Kenya 744 parent, no mildew occurred at any stage of growth. Lines that were segregating showed a ratio in the 2-leaf stage of approximately 3 resistant : 1 susceptible. Resistance apparently was completely dominant. In all the crosses, however, by the 4–5-leaf stage, some plants in the segregating lines were free from mildew, others had several pustules, and those that were susceptible as seedlings remained susceptible. It appears that as growth proceeds, heterozygous plants become slightly infected with mildew, but the homozygous resistant plants remain free at all times. Although no plants were selected from these F_3 lines and grown to F_4, this explanation seems reasonable, since in segregating F_3 lines, resistant, intermediate and susceptible plants occurred in approximately a 1:2:1 ratio.

In the four varieties mentioned, and in the 150 F_3 lines studied, there was complete agreement between seedling and adult plant reaction of homozygous lines to a single race of mildew. In heterozygous lines some differences were observed, but lines segregating as seedlings also segregated as adult plants. Exceptions to this may arise when more than one race of mildew is used to test hybrid material. In this study, lines were always inoculated with a single race. Kenya 744 may have other genes for resistance to specific races, although subsequent work at the University of Sydney has shown that the same gene in Kenya 744 gives resistance to this new race and to race 1 of *Erysiphe graminis Tritici.* Genetic factors that give resistance to specific races of powdery mildew have not been identified in wheat, but Honecker (1938) believes that resistance of certain barley varieties to several races of *E. graminis Hordei* is conditioned by the selfsame gene.

5. *Awn Development.*

The awn characters of each of the varieties studied are given in Plate ii, fig. 5. Kenya 744 is half awned, Kenya 745 and Dundee 985 are tip awned, and Federation 107 is bald. The awn development of F_1 plants and F_3 lines was studied in the field for all crosses, and F_2 plants of the cross Federation 107 × Kenya 744 were classified in the greenhouse. A single major factor was found to differentiate baldness from the half-awned type when Federation 107 was crossed with Kenya 744. Three hundred and fifty F_3 lines showed 84 were homozygous bald, 189 segregated for awn length between the limits of the two parents, and 77 were homozygous half awned. The P value for agreement with a 1:2:1 ratio lies between 0·20 and 0·30. A single major factor was also found for tip awn development in Kenya 745. On the basis of their breeding behaviour in F_3, 100 F_2 plants from the cross Federation 107 × Kenya 745 were found to be homozygous bald and 347 were tip awned, indicating a fairly good agreement with a 3:1 ratio. Transgressive segregation occurred for certain minor factors, since some awns of F_2 plants were one-half to three-quarters of an inch longer than the Kenya 745 parents, but no data were obtained on the number of these present.

It was apparent from the cross Kenya 745 × Kenya 744 that the two single major factors differentiating these varieties from Federation 107, were not allelic, and fully bearded types were obtained. Among 346 F_2 plants classified according to their breeding behaviour in F_3, 32 were homozygous for full beard, and 314 were either bald or intermediate between the two parents. On the assumption of a 15:1 ratio, the P value lies between 0·60 and 0·61. The crosses involving Dundee 985 could not be explained on this simple factorial basis, since in crosses with Kenya 744, an excess of fully bearded plants and a deficiency of completely bald plants, always showed up in F_2. When Dundee 985 was crossed with Kenya 745 no segregation for awn length occurred.

It appears from these data that Federation 107 has two factors for beardlessness, both of which behave as partial dominants in crosses with Kenya 744 and 745. One is allelic to the gene for half awnedness in Kenya 744 and the other is allelic to the gene for tip awnedness present in Kenya 745. Although Stewart (1925) reported these two factors linked with 35 per cent. of crossing over, the figures obtained by Churchward (1938) showed that they are inherited independently when Federation 107 is crossed with Hope, a fully bearded variety.

If the classification adopted by Watkins and Ellerton (1940) is used, the probable genotype of three of the parents used in this study are: Federation 107 $b_1^a b_1^a B_2 B_2$, Kenya 744 $b_1^a b_1^a b_2 b_2$, Kenya 745 $b_1 b_1 B_2 B_2$. According to this scheme it is clear that when Federation 107 is crossed with either of the Kenya varieties a single factor is indicated. In crosses between Kenya 744 and Kenya 745 the beardless class would be $b_1^a b_1^a B_2 B_2$, and the bearded class $b_1 b_1 b_2 b_2$.

6. *Grass Clump Character.*

McMillan (1937) has made an extensive study of the inheritance of grass clumps in crosses between varieties of *Triticum vulgare*. By using some of W. L. Waterhouse's data supplementary to his own, he found the varieties could be divided into five classes according to the type of segregation obtained in crosses. In these studies the genotype of Kenya 744 was found to be aBig, but that of Kenya 745 was not determined.

In connection with the problem of breeding for stem rust resistance in wheat at the University of Sydney, crosses have been made using as parents the two Kenya varieties reported herein, and many rust susceptible varieties. The genotypes of some of those parents are given in Table 18.

TABLE 18.
Grass Clump Genotype and Classification of Five Varieties of Wheat.

Variety.	Genotype.	McMillan's Class.
Kenya 744	aBig	IV
Kenya 745	—	—
Federation 107	abIG	III
Dundee 985	abIG	III
Nabawa	abIG	III
Bobin	AbIG	I

It has previously been reported that a ratio approximating to a 13:3 is obtained when Kenya 744 is crossed with Federation 107, Dundee 985 and Nabawa. These results were confirmed, as was the fact that grass clumps are obtained in F_1 when Kenya 744 is crossed with Bobin. The appearance of the F_1 plants and the approximate segregations obtained in F_2 are given in Table 19.

From this table it is clear that Kenya 745 does not give grass clumps in crosses with varieties representative of three of the five classes suggested by McMillan. Accordingly this variety has been placed in class V with supposed genotype bIg. Subsequent work has shown that certain other varieties of Kenya wheat also belong in this class.

7. *Association and Independence of Characters.*

(i). *Seedling and Adult Plant Resistance to Stem Rust.*—In previous studies attention has been given to the possibility of the correlation between the seedling

TABLE 19.

Appearance of F_1 Plants and the Approximate Segregations obtained in F_2 when Two Kenya Varieties were crossed together and with Four Rust Susceptible Australian Varieties.

Cross.	F_1.	Approximate Ratio in F_2.
Federation 107 × Kenya 744.	Normal.	13 Normals : 3 Grass Clumps.
Federation 107 × Kenya 745.	,,	All Normals.
Dundee 985 × Kenya 744.	,,	13 Normals : 3 Grass Clumps.
Dundee 985 × Kenya 745.	,,	All Normals.
Nabawa × Kenya 744.	,,	13 Normals : 3 Grass Clumps.
Nabawa × Kenya 745.	,,	All Normals.
Bobin × Kenya 744.	Grass Clumps.	No data.
Bobin × Kenya 745.	,,	All Normals.
Kenya 745 × Kenya 744.	,,	,,

reaction to a single race of rust and the reaction of adult plants to a collection of races. Two common wheats, Hope and H–44, are used very extensively in the United States and Canada as parents in crosses made for the purpose of obtaining new stem rust-resistant spring wheats. On material of this parentage no single race of rust is known which gives a reaction on seedling F_3 lines, similar to that given by a collection of races, when these same lines are tested in the field. From a cross of H–44 × Marquis, Neatby (1931) inferred that "lines susceptible in the seedling stage in the greenhouse to 15 forms used have as good a chance of being resistant in the field as have lines resistant to the 15 forms in the greenhouse". Crosses involving these two varieties as resistant parents show selection in the greenhouse to be of little value, since it will lead to the elimination of much material having adult plant resistance.

In the cross Federation 107 × Kenya 745, correlation between seedling and adult plant resistance was good, and better than the correlation obtained when Kenya 744 was the resistant parent. Tables 20 and 21 show the distribution of F_3 lines of the two crosses for their reaction at two stages of growth. Federation 107 × Kenya 744 material was not tested as seedlings in 1939, and the results obtained with the Federation 107 × Kenya 745 progenies for that year are essentially the same as for 1940.

TABLE 20.

Distribution of F_3 Lines of the Cross Federation 107 × Kenya 744 for Stem Rust Reaction to a Collection of Races in the Field in 1940, and for Seedling Reaction in the Greenhouse to Race 36.

Field Reaction to Many Races.		Seedling Reaction to Race 36.			
		Resistant.	Segregating.	Susceptible.	Total.
Moderately resistant	MR. ..	56	5		61
Segregating	MR-S.	4	84	6	97
	MR-MS.		1		
	MS-S.			2	
Susceptible	S.		5	42	47
Total		60	95	50	205

TABLE 21.

Distribution of F_3 Lines of the Cross Federation 107 × Kenya 745 for Stem Rust Reaction to a Collection of Races in the Field in 1940, and for Seedling Reaction in the Greenhouse to Race 56.

Field Reaction.		Seedling Reaction to Race 56.			
		Resistant.	Segregating.	Susceptible.	Total.
Semi-resistant	SR.	54	1		55
Segregating	SR-S... ..	3	127	1	134
	SR-MS. ..		1		
	MS-S. ..		1	1	
Susceptible	S.			52	52
Total		57	130	54	241

In the class segregating in the field, three sub-classes were found that have been grouped to give a ratio of 61:97:47 for field reaction, although, as previously indicated, the two MS–S families are probably homozygous susceptible. The P values for seedling and adult plant reaction agree well with a 1:2:1 expectancy, but there is no way yet of accounting for those cases where the reactions at two stages of growth are in disagreement.

From the F_3 seedlings of the Federation 107 × Kenya 745 cross a reaction to race 56 was obtained very similar to that given by these same lines when tested with a collection of races in the field. The figures indicate that probably one and the same gene gives resistance at both stages.

Race 56 serves to isolate as seedlings, lines of this cross that will be resistant or semi-resistant in the field. The same is true of races 1, 11, 14 (one culture), 15 (two cultures), 17, 21, 34, 36, 38 (two cultures), 47, 49, 59, 69, 80, 97, 117 and 147. Races 14A, 38B and a Brazilian culture of race 15 did not give reactions on F_3 seedlings in agreement with those produced by a collection of races in the field. As shown by the figures in Tables 9 and 10, lines selected as seedlings for resistance to race 19 may be resistant, but they could also be homozygous susceptible, when tested with race 56, either as seedlings or as adult plants. Results in close agreement with these were obtained when Dundee 985 was the susceptible parent.

(ii). *Seedling Resistance to Stem Rust and Awn Development.*—In the cross Federation 107 × Kenya 744, progenies of 314 F_2 plants selected at random, showed that the factor for seedling resistance to race 36 was inherited independently of the factor for half awnedness present in Kenya 744. A similar result was obtained when 499 random F_3 progenies of the cross Federation 107 × Kenya 745 were classified for resistance to race 56 and for the development of awns. It appears that the non-allelic factors for rust resistance present in the two Kenya varieties are inherited independently of the factors for awn development possessed by these parents. This was confirmed when 313 random F_3 lines of the cross Kenya 745 × Kenya 744 were inoculated as seedlings with race 17 and plants from remnant seed were classified for awns in the field. This independence of the factors concerned, is in agreement with results obtained by earlier workers with other varieties.

(iii). *Powdery Mildew and Seedling Resistance to Stem Rust.*—As in Table 22, it was apparent that resistance to mildew and seedling resistance to stem rust are inherited independently in the crosses Federation 107 × Kenya 744, Dundee 985 × Kenya 744 and Kenya 745 × Kenya 744.

(iv). *Powdery Mildew and Awn Development.*—In the greenhouse, F_2 plants of the cross Federation 107 × Kenya 744 were tested with mildew and grown to maturity, at which stage they were classified for an awn development. Random F_3 lines of the cross Kenya 745 × Kenya 744 were tested for mildew as seedlings, and classified subsequently in the field for awns. In both crosses, as shown in Table 22, the factors are inherited independently.

(v). *Seedling Resistance to Rust and Grass Clumps.*—Only greenhouse classifications were made on F_2 plants for resistance to rust and plant height. Two crosses, Federation 107 × Kenya 744, and Dundee 985 × Kenya 744, were studied. All factors concerned with grass clump production were inherited independently of the factor for resistance to races 17 and 36 present in Kenya 744.

(vi). *Powdery Mildew and Grass Clumps.*—As with the studies on stem rust and grass clumps, the studies involving the latter character and resistance to mildew were done solely in the greenhouse. Here again, the factors were shown to be inherited independently.

(vii). *Grass Clumps and Awn Development.*—Only one cross, Federation 107 × Kenya 744, was studied for the correlation of these two characters. As indicated in Table 22 the factors were inherited independently.

The complete results of the correlation of characters are given in Table 22. Seedling resistance to stem rust and resistance of adult plants appeared to be governed by the same factor, or factors very closely linked. The single factor present in Kenya 744 giving seedling resistance to race 17, was found to be inherited independently of the one present in Kenya 745 giving resistance to this same race. Both of these factors appear to be independent of those for mildew resistance, awn development and the grass clump character. It should be mentioned that other genes found in Kenya 745, such as those giving resistance to race 19 and semi-resistance to a Brazilian biotype of race 15, were not studied in relation to these other characters. The factors for mildew resistance, awns and grass clumps all appeared to be independent.

TABLE 22.

Range of P Values found when the Degree of Association of Several Characters was studied in Four Varieties of Wheat.

Cross.	Characters Studied.	No. of Plants or Lines.	Range of Value.
Federation 107 × Kenya 744 (lines)	Resistance to stem rust (field) and seedling resistance race 36	205	a
,, × ,, 745 ,,	,, ,, ,, ,, (field) and seedling resistance race 56	241	a
,, × ,, 744 ,,	,, ,, ,, ,, (seedling race 36) and awn development	314	0·80–0·90
,, × ,, 745 ,,	,, ,, ,, ,, (seedling race 36) and awn development	499	0·02–0·04
Kenya 745 × ,, 744 ,,	,, ,, ,, (seedling race 17) and awn development	313	0·01–0·02
Federation 107 × ,, ,, (plants)	,, ,, ,, ,, (seedling race 36) and powdery mildew)	423	0·50–0·70
Dundee 985 × ,, ,, ,,	,, ,, ,, ,, (seedling race 17) and powdery mildew	572	0·20
Kenya 745 × ,, ,, ,,	,, ,, ,, ,, (seedling race 17) and powdery mildew	229	0·90–0·95
,, ,, × ,, ,, (lines)	,, ,, ,, ,, (seedling race 17) and powdery mildew	342	0·50–0·70
Federation 107 × ,, ,, (plants)	,, ,, powdery mildew and awn development ..	517	0·70–0·80
Kenya 745 × ,, ,, (lines)	,, ,, ,, ,, ,, ,, ,, ..	323	0·70–0·80
Federation 107 × ,, ,, (plants)	,, ,, stem rust (seedling race 36) and grass clumps	403	0·20–0·30
Dundee 985 × ,, ,, ,,	,, ,, ,, ,, (seedling race 56) and grass clumps	559	0·50–0·70
Federation 107 × ,, ,, ,,	,, ,, powdery mildew and grass clumps ..	622	0·20–0·30
Dundee 985 × ,, ,, ,,	,, ,, ,, ,, ,, ,, ,, ..	658	0·20–0·30
Federation 107 × ,, ,, ,,	Awn development and grass clumps	529	0·30–0·50

a = P is very small.

DISCUSSION.

In areas where stem rust of wheat is prevalent, the varieties of wheat from Kenya Colony, East Africa, have provided breeders with a new and valuable source of stem rust resistance. The type of resistance possessed by these varieties is somewhat different from that shown by many other rust resistant parents. The two Kenya varieties used each showed the presence of a major factor for field resistance when they were crossed with Federation 107 and Dundee 985. The reaction of F_3 lines of adult plants in the field was found to be highly correlated with the reaction of seedlings of these same lines when tested to certain races in the greenhouse. Lines that would be homozygous resistant in the field in crosses involving Kenya 744, could be detected by inoculating the seedlings with race 36. However, when Kenya 745 was crossed with Federation 107, in addition to race 36, it was found that several other races would also serve to distinguish as seedlings lines that were homozygous for resistance of Kenya 745 in the field. These races were 1, 11, 14 (one culture), 15 (two cultures), 17, 21, 34, 38 (one culture), 47, 49, 56, 69, 80, 97, 117 and 147. Other races, however, such as 14 (one culture), 19, 38 (one culture) and 59 were of little use for this purpose since for seedling resistance to these races, Kenya 745 had a second factor additional to the one giving resistance to the above-mentioned group of races. By selecting for resistance to this latter group of races, those homozygous resistant would not always give this same reaction when tested with such races as 17 and 56. On the average, one line out of every four selected for resistance to race 19 would be resistant also to race 56.

However, all lines resistant to race 56 would also give that reaction when tested with race 19. In this way, some races can be designated key races, and when resistance to them has been incorporated into new varieties, it can confidently be expected that such varieties will be resistant to many other races.

It is probable that in many parental varieties one or two major factors give resistance to a large number of races. Such has been found to be the case in Hope, H–44, Gaza and several varieties from Kenya Colony. Selections made from crosses between these parents and susceptible types have been grown under epidemic conditions in New South Wales for many years, and the field resistance possessed by them has been obtained by selecting virtually to one race, namely, race 34. However, when some 500 such selections were tested, either as seedlings or adult plants, with a collection of races in the United States, they continued to show resistance. If preliminary fundamental work can lead to a classification of the races present in any particular area, then much work will be avoided if eliminating tests on segregating material are made with one race, rather than with all those known to occur in the district. It would appear, then, that the multiplicity of rust races present does not present an insurmountable barrier to the plant breeder. Once the constitution and the variability of the rust flora is known, the breeding programme can proceed according to plan, provided new unrecorded races or biotypes do not arise which are capable of attacking the original parental stocks.

It is of some interest that two varieties of wheat having their origin in Kenya Colony should possess different factors for seedling resistance to race 17 of stem rust. The fact that this does occur should be helpful if it is desired to incorporate the resistance of several varieties into a new hybrid. New varieties having their resistance made up from several sources would be expected to have resistance to a wider range of races of stem rust, but there is no evidence to show that different factors for rust resistance to a single race will be cumulative in their effect. The situation may arise where the addition of other genes for resistance, to an already resistant type, will actually lead to a lowering of its resistance.

In addition to their rust resistance, some varieties of wheat from Kenya Colony have a useful resistance to flag smut, and in areas where summer temperatures are not too high, they should be valuable parents. At the University of Sydney they have been found to possess a very satisfactory combining ability, and high yielding segregates have been derived from the crosses in which they have entered as one parent.

SUMMARY.

Two varieties of wheat, Kenya 744 and Kenya 745, were each found to have a valuable resistance to many races of stem rust. This resistance was controlled mainly by a single major factor in each variety. Seedling and adult plant resistance to rust was highly correlated, but the factors governing it were not allelic in these two varieties. Kenya 745 has a single major factor, K_1, for resistance to races 1, 11, 14 (one culture), 15 (two cultures), 17, 21, 34, 36, 38 (one culture), 47, 49, 56, 69, 80, 97, 117 and 147, but apparently two factors, K_1 and K_2, unequal in their effect, operate against races 14 (one culture), 19, 38 (one culture) and 59, the more effective of these factors being K_1, which gives resistance to races in the larger group. F_3 lines selected for resistance to any race in the first group, therefore, will be resistant to others in that group, and at the same time will be resistant to races in the second group. However, lines selected for resistance to the second group of races cannot be expected always to give resistance to races in the first group. Race 14 and race 38 contained biotypes which on the differential varieties gave reactions typical of the race concerned. Two such biotypes could be distinguished in each race, since tests on F_3 lines indicated that Kenya 745 had one factor for resistance to one biotype, and two factors for resistance to another biotype of the same race. Kenya 744 was resistant to stem rust and powdery mildew; it was half awned, and grass clumps appeared in F_2 when it was crossed with Federation 107. The factors governing these characters were all inherited independently, as were the factors for stem rust and tip awns of Kenya 745. Transgressive segregation for awns occurred when the two Kenya varieties were crossed.

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EXPLANATION OF PLATE II.

Fig. 1.—Showing the stem rust reaction of four varieties of wheat in the field at St. Paul. A, Kenya 744 (1939); B, Kenya 745 (1939); C, Kenya 744 (1940); D, Kenya 745 (1940); E, Federation 107 (1939); F, Dundee 985 (1939).

Fig. 2.—Showing the difference in severity of attacks of stem rust on Kenya 745 and hybrids in 1939. A, Kenya 745, northern or shady side; B, Kenya 745, southern or sunny side; C-F, Flattened stems of hybrid plants. The left side in each case was on the southern side of the stem.

Fig. 3.—Stem rust reaction of seedling leaves of Kenya 744 and 745, and F3 lines of a cross between them. A, Kenya 745; B, Homozygous resistant line; C, Segregating line; D, Homozygous susceptible line; E, Kenya 744.

Fig. 4.—Reaction of two varieties of wheat to three biotypes of race 15 of stem rust. A, Brazilian; B, Japanese; C, United States. In A, B and C, Kenya 745 is on the left (two leaves), and Federation 107 is on the right.

Fig. 5.—Awn types. A, Kenya 744; B, Kenya 745; C, Dundee 985; D, Federation 107.